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THE HETEROTYPIC MATURATION MITOSIS IN AMPHIBIA AND ITS GENERAL SIGNIFICANCE.

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The marked contradiction between the results of workers on spermatogenesis of vertebrates, and of those on the spermatogenesis of arthropods, has led me to examine the formation of the chromosomes of the first maturation mitosis in urodele amphibia. The question at issue is of course the interpretation of the heterotypic division, for if that is an equational division as generally maintained, then in vertebrates there would be no transverse, or so-called "reduction," division of the chromosomes. Much time and thought has been given to the interpretation of the various ring-shaped chromosomes of heterotypic divisions, *i. e.*, as to whether the space enclosed by the ring represents a longitudinal split of a single chromosome, or a space between two univalent chromosomes. Uncertainty and confusion has resulted, because most of these interpretations have not taken into account the earliest stages in the formation of such chromosomes, which are really the only stages that need critical examination.

The two species in which these decisive periods of the spermatogenesis was studied, are *Plethodon cinereus* (Green) and *Desmognathus fuscus* (Raf.); the maturation mitoses occur in the summer, and the testes were fixed in Hermann's and Flemming's solutions, and stained with iron haematoxyline. The spermatogenesis is essentially alike in both; Figs. 1-6 are camera drawings of spermatocytes of *Desmognathus*, and 7 and 8 of *Plethodon*.

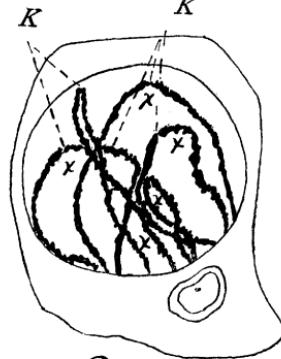
The normal number of chromosomes is twenty-four as shown clearly on a pole view of a monaster (equatorial plate) stage (Fig. 1); in this figure four of the chromosomes are cross-sectioned, and one of the others shows very clearly the longitudinal split. In the spermatocytes which result from the last spermatogonic division there is just half this number of chromosomes, namely twelve, the so-called reduction in number taking place



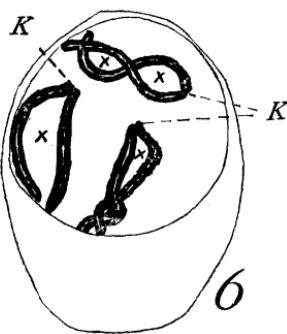
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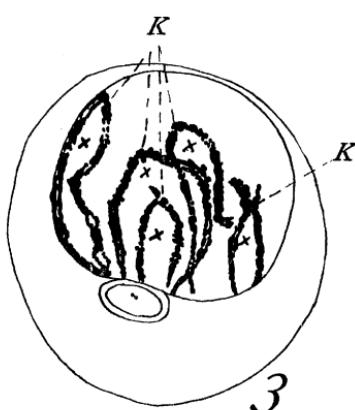
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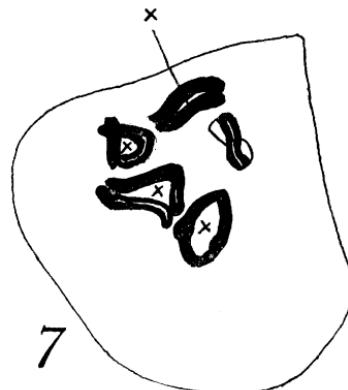
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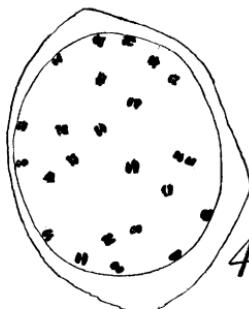
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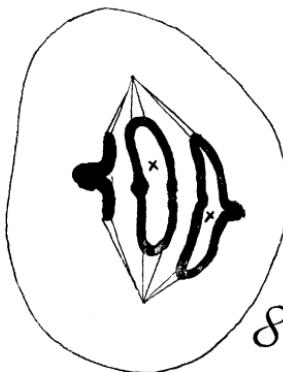
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8

in the synapsis stage of the growth period before the maturation divisions. Now what has to be determined is the changes that occur in these chromosomes in the prophases of the first maturation mitosis. In the early prophases (Figs. 2, 3, 5) these chromosomes always show a definite arrangement; in the figures only a few of the chromosomes are shown in each case, namely those which are seen in their entirety in the plane of the section. There is a distinct polarity of cell body and of chromosomes, and it is the same polarity which I found to obtain in the spermatocytes of *Peripatus*: the nucleus lies in the portion of the cell where there is the least amount of protoplasm, and the sphere (idiozome body) at that side of the nucleus directed towards the greatest protoplasmic mass. For these two poles, as a translation of Rabl's "Pol" and "Gegenpol," I used in the case of *Peripatus* the terms "central pole" and "distal pole," and these terms may equally well be applied to the amphibian spermatocytes. The arrangement in the case of the chromosomes is well shown in the Figs 2, 3 and 5. Each chromosome has the form of a loop like a U or a V with the bend or angle of the chromosome pointing towards the central pole, and the free ends terminating at the distal pole of the nucleus; sometimes at these early stages the two free ends of a chromosome may be applied together so that the whole chromosome has the form of an elongated ring; but generally in these early prophases the U or V shape is the prevalent one.

There are just twelve of these looped chromosomes, half the number of those in the spermatogonia, as may be determined by study of cells cut in a plane at right angles to the axis connecting the central and distal poles. Thus in Fig. 4 (corresponding to the stage of Fig. 3) can be counted twenty-four cross-sections of chromatin threads, every two of which represent the two arms of one of the twelve looped chromosomes. Now the point of great importance is that these early U and V-shaped chromosomes have not arisen by any longitudinal splitting of a single chromosome, for in the very earliest prophases, even earlier than that represented in Fig. 2, they have this shape; therefore the space circumscribed by the two arms of the chromosome does not represent a longitudinal split, but a longitudi-

nal split appears later and then along the axis of each arm (Figs. 3-6). What then is the correct interpretation of each chromosome loop? Each U or V is, first of all, a bivalent chromosome, since they occur in half the number of the chromosomes of the spermatogonia. Second, each arm of one of these bivalent chromosomes represents one of the univalent chromosomes of the spermatogonia. In the case of a bivalent chromosome of the form of a U or V, the two univalent chromosomes are connected together at the angle, that is one end of one chromosome is joined to one end of another chromosome; these points of union are marked in the Figs. 2, 3, 5 and 6 by the letter *K*. Just at this point of junction can be seen in many cases, though not so clearly as in *Peripatus*, a broad connecting linin thread, as in the chromosomes of Fig. 5. When a bivalent chromosome is an elongate ring, as in the case of the left-hand one of Fig. 3, then both ends of both univalent chromosomes are connected. The bivalent chromosomes of *Desmognathus* and *Plethodon* thus represent each two univalent chromosomes joined end to end, and the space between the two arms of a bivalent chromosome is the space between two univalent chromosomes, whether this space be bounded by a chromosome of the form of a U, a V, or an O. This is the space marked in the figures by the letter *x*, and, as the present observations show, does not represent a longitudinal split since it is widest at the earliest stages of the prophase.

The longitudinal splitting of the chromosomes is shown in its commencement in Fig. 3, where certain microsome groups are splitting ahead of others. Fig. 5 shows the stage where this split is most pronounced. Fig. 4 shows the split on cross-sectioned chromosomes. It is still apparent in some of the chromosomes of Fig. 7, but in the equatorial plate stage (Fig. 8) is hidden, to reappear at the anaphase as a longitudinal split of each of the daughter (univalent) chromosomes. This temporary disappearance of the longitudinal split during the equatorial plate stage of the first maturation mitosis has been noted in various objects, and I have described it in detail for *Peripatus* and the *Hemiptera*, as has Korschelt for *Ophryotrocha*. Along the plane of this split the daughter chromosomes divide in the second maturation mitosis, so that the latter is an equation division.

It is then apparent that the split along each arm of a bivalent chromosome, is a longitudinal split of each univalent chromosome, and is a preparation for the second maturation mitosis. It is equally evident that the space marked x in the figures does not represent any longitudinal split, but a space between two univalent chromosomes. Hence in the typical chromosomes of the ring form, as shown in Fig. 8, the space enclosed by the chromosome is the space between two univalent chromosomes, and has nothing to do with the longitudinal split. The thickenings so frequently found upon the rings, as in Figs. 7 and 8, are the points of union of the ends of two univalent chromosomes, as becomes clear from the intermediate stages shown in Figs. 6 and 7, and are not, as generally interpreted, portions of the chromosome where the longitudinal split is least evident. The reader may follow the spaces marked x in the chromosomes from the stage of Fig. 8 back through successive stages to Fig. 2, to be certain of this fact. And it is decisive that this space becomes wider the earlier the prophase, as a comparison of Figs. 8 and 2 shows, and does not lead back to a simple longitudinal splitting.

So the form of the bivalent chromosomes is explained, and the fact established that the heterotypic mitosis, the first maturation mitosis, is not an equational division but separates entire univalent chromosomes, while the second maturation mitosis is equational.

These views are in disagreement with the conclusions of most other workers on amphibian spermatogenesis, because the writers have mostly assumed that the space marked x in my figures, the space enclosed by the ring, is a longitudinal split. Flemming first described the heterotypic mitosis and named it; he overlooked the true longitudinal split in each arm of a bivalent chromosome, and concludes the space enclosed by the definitive chromosome to be the longitudinal split. Vom Rath described in *Salamandra* a reduction division on the basis of tetrad formation with spherical chromosomes, but later observers have demonstrated that he studied abnormal mitoses. Meves essentially corroborates Flemming's interpretations, but he did not note the polarity of the spermatocytes as evidenced in the arrangement of the chromosomes, though it is shown in his Fig. 47, Pl. IV., and hence leaves untouched the question of the origin of the bivalent

chromosomes ; he also failed to describe the true longitudinal split in each arm of the chromosomes, though certain of his figures show it indistinctly. McGregor confirmed for *Amphiuma* Meves' account for *Salamandra*, but likewise failed to show how the bivalent chromosomes are produced ; his Fig. 7, Pl. IV., shows the true longitudinal split, but it is not demonstrated by his figures that this becomes the space enclosed by the definitive chromosome. Eisen likewise interprets, for *Batrachoseps*, the heterotypic division as an equation division, though his "bouquet stage" is essentially similar in its details to my Fig. 2, and though his results might equally well be interpreted as speaking for a transverse division. Kingsbury's account for *Desmognathus* is clearly a careful study ; his Figs. 4 and 5 may be compared with my Figs. 4 and 3 ; he found the polarity of the chromosomes in the nucleus, saw the true longitudinal split (his Fig. 6), but illustrates no stages to show that this split is connected with the space in the definitive chromosomes. Janssen's account for *Triton* appears to be the most detailed and careful, his Figs. 4, 5 and 32 show appearances of the early chromosomes just as I have found ; he describes the synapsis stage where the formation of bivalent chromosomes takes place ; he was the first to clearly recognize this stage in the Amphibia, but holds the bivalent chromosomes undergo two longitudinal splittings after their transverse segmentation from a continuous chromatin spirem.

In the ovogenesis of Amphibia, to mention only two more recent studies, Lebrun concludes that both maturation divisions are equational, though more on the basis of a lengthy discussion of the definitive forms of the chromosomes than of a description of the early formation stages. Miss King, for *Bufo*, was unable to determine whether the heterotypic division is transverse or equational.

The whole question is one of a careful interpretation of the early stages of the chromosomes, and the mode of formation of the bivalent chromosomes. The workers on this subject have been satisfied for the most part to know that in the spermatocytes the chromosomes are bivalent, without describing the mode of union of every two univalent chromosomes. In *Desmognathus* there is one true longitudinal split, and besides that what has heretofore

been regarded as a second longitudinal split but what is really the space between the two univalent chromosomes of a pair.

The term "reduction division" was introduced by Weismann, to denote a division that separates entire chromosomes, in contradiction to "equation division" which halves longitudinally each chromosome. Weismann, in his splendid conclusion that such a division would be found to occur, unfortunately assumed that there must be a doubling of the normal number of chromosomes before the maturation. This doubling does not occur, as Boveri and Brauer were the first to demonstrate, but instead there is in the synapsis stage, as I first showed, a union of chromosomes end to end in pairs. This union is not due, as Rückert suggested, to the chromatin spirem breaking into half the somatic number of chromosomes, since there is no continuous *chromatin* spirem in the prophases of the maturation mitosis in any of the objects studied by me, but is a union of chromosomes that were disunited before.

That a separation of entire univalent chromosomes in one of the maturation divisions does occur, is shown by the following studies: Rückert and Häcker for the ovogenesis of Copepoda, finding the separation of entire univalent chromosomes to occur in the *second* division; while Lerat does not decide whether such a division occurs, but points out that it is the *first* division which is heterotypical. In the spermatogenesis of *Gryllotalpa*, by Vom Rath; of Hemiptera, by Henking, myself and Paulmier; of Orthoptera by McClung, Sutton, and Wilcox. The first maturation in the ovogenesis of *Ophryotrocha*, according to Korschelt's account, also separates entire univalent chromosomes, and very clearly the first maturation in the spermatogenesis of *Peripatus* according to my own observations. For the ovogenesis of *Limnæa* this is maintained by Linville, but the chromosomes in this object are unfavorable for decisive interpretation. In Isopoda (*Oniscus*) the first division was shown to be reductional by Miss Nichols. For *Thalassema* and *Zirphæa* the same conclusions were reached by Griffin; and Lillie considers it possible that Griffin's mode of interpretation may be applied to the egg of *Unio*. Van Winiwarter in a very excellent detailed study of these stages in the ovogenesis of mammals (*Homo, Lepus*), considers it

probable that one of these divisions is reductional. Schockaert, for the ovogenesis of *Thysanozoön*, finds also a reduction division, in contradiction to the earlier work of Van der Stricht. Finally, Carnoy's earlier work speaks very strongly for the occurrence of reduction divisions.

It is then very humorous to read in a recent paper by Meves : "Ich für meine Person halte es aber, heute mehr als je, für gerechtfertigt, das Vorkommen sogenannte Reduktionsteilungen zu bezweifeln." Herr Meves has the right to hold any opinion he pleases, but he will soon find himself in the small minority where dogmatic assertion takes the place of fair-mindedness. As the pupil of Flemming, Meves must stand by his teacher, to the effect that there occur only equational divisions. Herr Meves has had very little experience in the field of the phenomena of maturation, though he has done excellent work in the study of the formation of the spermatozoon, and in his paper on the spermatogenesis of *Salamandra* overlooked all the phenomena which are decisive in regard to a reduction division. I might add, "ich für meine Person halte Herrn Meves' Resultate unbewiesen zu sein."

In the light of the recent work it becomes apparent that "heterotypic" division is synonymous with "reduction" division ; it is heterotypic in being the only mitosis in the germinal cycle in which entire univalent chromosomes are separated in metakinesis. This explains why the shape of the chromosomes in this mitosis differ from all other mitoses ; if it were an equation division, why should its chromosomes differ so markedly from those in other equation divisions ? "Transverse," "reduction" and "heterotypic" divisions express the same phenomenon in different words, and the nail is driven home when the facts are so clear in amphibian spermatogenesis, in the very cells which were held to disprove the occurrence of reduction mitoses.

In my paper on *Peripatus* I proved that the bivalent chromosomes are produced by the union end to end of every two univalent chromosomes, and not by a splitting of a chromatin spirem into half the normal number of segments. This has since been found by several observers to be the case for other objects. Then in a paper, "The Germ Cells of the Metazoa," I showed

that each bivalent chromosome is very probably formed by the union of a paternal with a maternal chromosome, and interpreted this process as part of the phenomenon of conjugation, as a conjugation of the chromosomes. I showed also that when in the spermatogonia certain chromosomes can be distinguished from the others by peculiarities of size, that such chromosomes pair together in the synapsis; this was the case in *Protenor*, *Peliopelta* and *Zaitia*. McClung (1902) has noted a similar case for *Anabrus*. A few months ago Sutton confirmed these conclusions for *Brachystola*, and on the basis of a careful examination of the chromosomes has reached the important conclusion, that, maternal chromosomes of a certain length uniting always with paternal chromosomes of the same length, the result of the reduction division, in separating such two univalent chromosomes from each other, prevents the retention by either of the daughter cells of two chromosomes representing the same characters. Such a result is a strong confirmation of the brilliant postulates of Weismann.

If it be true that wherever a heterotypic mitosis occurs, it denotes the separation of entire univalent chromosomes, then the old strife of whether a reduction division does or does not take place in the maturation of the germ cells is decided in the affirmative, and we are no longer met by the discrepancy of certain animals with and certain without a reduction division. It rests with the opponents of this view to prove that the heterotypic division is an equation division, and that has not yet been satisfactorily done. And in reaching this conclusion I may state frankly that at the outset of my studies I was fully convinced, almost as much as Herr Meves himself, that the heterotypic mitosis is an equation division; only long observations have shown me that it can only be regarded as a reduction division.

McClung has recently (1902) made an embittered attack upon my studies on spermatogenesis, due in large part to a misunderstanding of my position. He states at various places that my views are conflicting, and that he is unable to harmonize them. Certain serious mistakes I made in my first paper (1898) I took pains to correct in two others (1899, 1901), and in these my position is stated very definitely and without contradictions.

Were he as frank in admitting mistakes, there would be great unanimity.

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